Larval and Post-Larval Stages of *Jasus lalandii* (Milne Edw.), Ortmann.

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[Plates 12–17, and 12 Text-figures.]

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In the Journal of the Linnean Society, Zoology, vol. xxxii. October (1913), p. 225, I described the newly-hatched larva of *Jasus lalandii*. Since then sufficient material has been procured to give a fairly complete account of later stages. This includes the immediately succeeding stage (1·7 mm. in length), numerous specimens of which were got by rearing from the egg and by tow-netting in Table Bay, a much less numerous series procured further from the shore (from 3·8 to 37 mm. in length), and, finally, a number of specimens of the "puerulus" stage (from 22 to 26 mm.), and of succeeding stages in which the cuticle becomes calcified.

That all these are stages of *Jasus lalandii* seems probable from their general resemblance, and from a comparison with phyllosomas found at other places on the South African coast. The evidence from locality is also particularly trustworthy, owing to the distribution of the Cape crawfish and other South African Loricata. *Jasus lalandii* is abundant on the west coast from Cape Point northwards, but to the east of this it is very scarce, and has not been found on the east coast north of Port Elizabeth. On the south coast a *Palinurus* has been found, but it is not abundant. On the east coast a *Panulirus* is fairly abundant, and *Scyllarides* is common in Natal waters. The phyllosomas referred to *Jasus* have all been found on the west coast. Three other kinds have been procured from the south and east coasts: one, which grows to a very large size, is, on the evidence of its flat tentacles, referable to *Scyllarides*, the other two probably to *Palinurus* and *Panulirus*. The puerulus stages referred to *Jasus* have all been found in Table Bay; two other kinds, obviously different, have been found on the east and south coasts and are probably referable to the other South African Loricata mentioned—one with a pair of ventral spines to *Palinurus*, and the other with long antennular flagella to *Panulirus*.

In the following account a more detailed description of the first or "naupliosoma" stage, for purposes of comparison, is given; a typical phyllosoma stage of 1·7 mm. is described; succeeding stages of 3·8, 24, 26, 33, 35, and 37 mm. are then described in such detail as seems necessary, and, lastly, some points, which seem to be of significance, are noted in the "puerulus" stage.

The Nauplosoma.

For comparison with later stages, further details with figures, of the appendages, may be given. (I may here note incidentally that the name suggested as convenient to denote this stage was not intended to suggest any connexion with the nauplius stage, which, as stated, has presumably been passed long before in the development of the embryo. The name was given on account of the apparent resemblance of this stage, when seen in the living condition, to a nauplius; it was not intended to suggest any direct relation to the nauplius stage, and, in so far as it does so, is inappropriate.)

The *antennules* (Pl. **13.** fig. 1) are as described, and it may be added that, in addition to the stout terminal spines under the cuticle, the long filamentous processes, described in the next stage, can also be made out, though not clearly, as they are coiled up under the cuticle.

The *antennæ* (Pl. **13.** fig. 2) are also as described. The protuberances at their bases seem, on further examination, to be due to the presence of the antennal gland.

The *mandibles* (Pl. **13.** fig. 3), as viewed from below, are short limbs, bent inwards at their tips, which end in a tridentate spine. When they are dissected out and viewed from the posterior or anterior aspect, the spine is seen to be the first of a series, which extends inwards towards the body and ends in a separate group of small stout spines. The whole is covered by cuticle, and as the general arrangement of these spines does not differ essentially from that in the largest phyllosomas, they will be described there in more detail.

The *first* (Pl. **13.** fig. 4) and *second maxillæ* (fig. 5) are as described.

The rudimentary *first maxillipede* (fig. 6) does not appear to have a cuticle covering its single spine at this stage.

The *second maxillipede* (fig. 7) consists of five distinct segments: the first is short and is followed by a long one; the third is again short, the fourth is longer, and the fifth is small and terminated by about four spines under the cuticle.

The *third maxillipede* (fig. 8) has also five distinct segments, the first short, the second very long, and, at its proximal end, coiled or folded on itself, there being about two such distinct coils or folds; the third segment is short, straight and not coiled, as are also the fourth and fifth, the last having some spines under the cuticle. The whole appendage is bent in the form of an irregular **S**, and, in its normal position lies, compactly folded up, under the succeeding appendages, which are arched forward over the ventral side of the body.

The *first pereiopod* (fig. 9) has the first two segments broad, comparatively short, and well provided with muscles; the strong spine, so well developed in the phyllosoma on the first segment, does not appear. In the second the

muscles, destined to control the active movement of the exopodite in the next stage, are specially marked. The endopodite is much coiled on itself, so that it is not very much longer than the exopodite. Such coiling occurs at the proximal end of the first segment, where the limb is completely bent on itself, the remainder of its length being quite straight. The second segment of the endopodite is relatively short and straight; the third is the most coiled, there being one or two complete coils, gradually passing into mere undulations, and eventually into the straight distal part of the segment. The last segment is short and straight. The exopodite is not shortened by such coiling of the limb under the cuticle; it is already divided into segments more or less distinctly, but there are no swimming setæ.

The *second pereiopod* (fig. 10) is very similar to the first.

The *third pereiopod* (fig. 11) has the first two segments well developed and somewhat similar to those of the preceding appendages; the second, however, is rather slender, slightly coiled, and not marked off clearly from the succeeding. It also has the rudiment of an exopodite at its distal extremity. The first segment of the endopodite is long, somewhat slender, and coiled at its proximal extremity, the second is short and straight, but the third is long and very much coiled at its proximal end for a little over half its length.

The *fourth pereiopod* is represented by a slight swelling between the base of the third and the commencement of the abdominal region. In *Palinurus vulgaris* the fourth and fifth pereiopods are present on hatching.

Phyllosoma of 1·7 mm. [Fig. 12] Pl. 14.

The stage succeeding the naupliosoma is the characteristic phyllosoma, with transparent body, without the locomotory setæ of the antennæ, and provided with locomotory setæ on the exopodites of the walking-legs. The spines and setæ covered by cuticle in the last stages are now exposed, and the appendages, which were formerly coiled up under the cuticle, now become straight and about double their former length. Though this transformation is thus effected at a single ecdysis, there is no stage at which the larva is not provided with active swimming organs, for, as was observed, the cuticle with the swimming setæ of the antennæ is shed some time after that of the other appendages, so that by the time these were lost those of the exopodites of the pereiopods were in full activity.

The body is now transparent, being devoid of yolk-granules, though some may be seen in the intestine in the abdominal region. There are also present the characteristic red pigment spots seen in the naupliosoma, and present even in the embryo before hatching.

On the under side of the body a number of closely-set small projections were seen under the microscope. These cover the whole of the ventral side of the thorax, from the third maxillipedes to the beginning of the abdominal

region, but do not extend on to the bases of the walking-legs. They consist of minute dome-shaped cuticular elevations, at the apex of each of which there is a fine hair-like process about double the length of the basal portion. They occur, but more sparsely, on the ventral surface of the head region from the base of the antennæ backwards. Such fine (sensory?) setæ do not seem to have been observed on any other phyllosomas.

The diverticula of the liver can be readily seen in the transparent thorax. There are three on each side, a long one running forward on each side of the œsophagus almost to the antennal gland, a much shorter one projecting backwards, and a large trilobed lateral one. The condition, however, is not different from that in the naupliosoma stage, in which the liver can be easily seen in suitably stained specimens.

The segmentation of the body can be made out very clearly in some specimens. It consists of one distinct segment in the thoracic region—namely, the second thoracic, to which the second maxillipedes belong. Four segments can be clearly distinguished in the abdominal region in some specimens.

The eyes stand more out from the body, the peduncles being straighter, more elongate, and with their bases somewhat nearer each other.

The *antennules* (Pl. **13.** fig. 13) present a marked difference from those of the naupliosoma. This is chiefly in the appearance of three long filamentous projections. They do not project forward in the same axis as the antennæ, but are, somewhat abruptly, curved downwards. The other shorter, but similar filaments were seen at their bases. They are not of the same appearance as the ordinary spines, two of which also occur at the extremity of the antennule. They were not seen in any of the phyllosomas of a larger size, but may occur there also, as they are very readily broken off. It may be suggested that they are of a sensory nature, especially as in stained specimens a group of what appeared to be nerve-cells occurs near their bases. Near the distal part of the antennule is a strong spine, and a similar one occurs a short distance behind it. There are, in some specimens, slight traces of a single division in the antennule.

The *antennæ* (fig. 14) have also changed considerably, chiefly in the absence of the long swimming setæ.

In a very few, apparently just after ecdysis, the exopodite still retains the indentations on its posterior border at the points of insertion of the setæ, but in most these are absent. The endopodite shows a marked advance. It is now longer than the exopodite, a division appears forming a proximal section, about one-fourth of its length. This is followed by a second section, terminated by two or three spines, and, lastly, follow the rudiments of the flagellum, about a third of the endopodite in length and already provided with small setæ. It may be noted that the endopodite and exopodite have apparently changed positions (*cf.* fig. 2), and at first it appeared as if the

flagellate branch was the exopodite, but this was clearly seen not to be the case, as in some specimens the non-flagellate branch still possessed the indentations of the swimming setæ. A certain amount of torsion therefore takes place in the antenna when it comes to take up a more anteriorly directed position in the phyllosoma.

The *mandible* (fig. 15, *md.*) now shows more clearly the outer tridentate spine, followed by a ridge of spines passing inward, and separated by an interval from a raised portion provided with small short spines. This arrangement does not seem to differ from that in the larger phyllosomas.

The *first maxilla* (fig. 15, *mx.* 1) consists of a short, stout, basal part, inserted immediately behind the base of the mandible. Its two short branches are each provided with two long, stout, and curved setæ, on which are secondary setæ, giving them a plumose appearance. In shed cuticles the cleft between the two branches is seen to be much deeper than appears in the complete animal, and a basal part can hardly be recognised. They are commonly regarded as two segments of the protopodite.

The *second maxilla* (fig. 15, *mx.* 2) is about ·11 mm. in length, blade-like, and usually shows no division. It is attached to the body by a relatively narrow base, but soon broadens out into a flat expansion, the posterior border of which is straighter than the anterior, which is provided with a single spine about half the diameter of the blade, and situated at about the middle of its length. The appendage ends in a knob-like projection, provided with four very long plumose spines, about double the length of the appendage. This little knob is of interest, as it is destined to become the scaphognathite. In some specimens it is clearly defined by a constriction at its base.

The *first maxillipede* (fig. 15, *mxp.* 1) is very small, and consists of a little hillock-like projection about ·006 mm. in diameter and height. It has a long spine projecting from its apex, as in the naupliosoma stage, and, in fact, has not apparently altered. It is to be noted that it is here well separated from the base of the second maxilla, for, when it reappears after an apparent absence in the next stage, it occupies a different position.

The *second maxillipede* (Pl. **13.** fig. 16) consists of five distinct segments. The first is short, the second about four times its length, the third equal to it, the fourth slightly longer and somewhat larger than the last. There are no spines on the first and third, but on the second there is a well-marked one, about the middle of its length. At the distal extremity of the fourth there are five long spines, each provided with spinules on its inner side. The last segment is terminated by a long curved spine devoid of spinules. At its base are four small spines. The whole appendage reaches to about the anterior third of the head region.

The *third maxillipede* (fig. 17) consists of six distinct segments, the first short and provided with a long broad spine, directed downwards and inwards. The second segment is long, and has two or three spines at its distal end, but

no trace of an exopodite. The third is slightly longer, the fourth short and terminated by three or four spines. The fifth is long, and has six spines on its distal half, the first near the middle, the second small and serrate. The third to sixth are long and differ from other spines noted in being recurved at their tips, which are provided with retrorse spinules, so that when the last joint is bent backwards between them, in the manner of a subchela, they form a most effective grasping and retaining organ. The end of this segment is provided with four long spines with antrorse serrations. The last segment is short and ends in a long spine, at the base of which are two long spines, all antrorsely serrated. The whole appendage may extend beyond the tips of the antennæ.

The *first pereiopod* (fig. 18) has a stout basal portion, its breadth being about two-thirds of its length. It is provided, like the basipodite of the preceding and following appendages, with a long spine. Such spines are not serrated and are bent downwards and inwards towards the middle line of the body. The second segment is longer, but also stout, well provided with muscles, and has a spine on the dorsal side at its distal end. The first segment of the endopodite is slightly longer than the last and has two spines near its middle; it ends in three or more spines. The second segment of the endopodite is smaller, and has one large spine and two small ones at its extremity. The third segment is very long, being about four times the length of the preceding, and there are about ten long serrated spines scattered over its length; nearer to its distal extremity there is a group of four, whose bases are close together in a transverse line, and at its end, where it articulates with the last joint, is a group of about six. The last segment is short and ends in a long spine with two shorter ones at its base. The exopodite consists of a long proximal segment, with two spines near its middle and one at its distal extremity. The remainder of its length is divided up into short segments provided with long plumose setæ.

The *second pereiopod* (fig. 19) is similar to the first.

The *third pereiopod* (fig. 20) has the first segment short and stout, with a long spine as in the preceding limbs. The second segment is long and has a triangular leaf-like projection (the exopodite) at the beginning of the distal third. Three spines, one before and two after the exopodite, occur at this point, but the segment which appears in the next stage is, as yet, not to be seen. At the distal end there are two spines. The third and fifth segments are much longer than in the other legs.

Occurrence of Phyllosoma of 1·7 *mm.*

The first phyllosomas are readily procured by keeping crawfish with berry in a well-aerated aquarium. So far there has been no further success in the rearing of the young, no decidedly later stages having been observed in confinement.

This stage was also readily found in the sea. A series of eighty-five tow-nettings were taken at more or less regular intervals in Table Bay from January 1913 to May 1914, and numerous specimens were procured at certain times of the year. In all of these (over several thousands in number) no later stage was observed. The explanation of this may be that, in casting their cuticle at this stage, they go to the bottom, and this seems to be indicated also by the sudden disappearance of the phyllosomas from the tow-nettings after the 10th February, 1914, previous to which they were numerous. The procuring of a few cast cuticles on the 12th of the same month is also significant. These cast cuticles were quite identical in size and general character to the phyllosomas. Some of the tow-nettings had perfect phyllosomas together with cast cuticles, but no trace of the animals which had shed the cuticle.

Habits and Behaviour of Phyllosomas of 1·7 *mm.*

On hatching the naupliosoma rapidly ascends to the surface by means of its setose antennæ. The head region is uppermost and the antennules project upwards. The plane of the exopodite and endopodite and of the large parachute-like group of swimming setæ is mostly horizontal, and this is effected by the exopodite projecting toward the back of the body, one endopodite in a lateral direction. When the larvæ reach the surface they can progress in a horizontal direction, and they then seek out the most illuminated part. In a few hours (4–6) the phyllosoma stage is assumed. The legs are very much longer and project laterally, the exopodite upwards, the endopodite downwards and inwards, except in the case of the third, which projects out straight behind the body. The two pairs of exopodites of the first and second pereiopods are in active movement, and the long plumose setæ with which they are provided would appear to be very effective swimming organs. This, however, is not the case and the forward progress of the body is comparatively slow. From a purely mechanical point of view, they seem badly adapted for progression, as they project well over the centre of gravity of the animal, and their characteristic lashing movement (if too energetic) would result in the body turning a somersault—in fact, this occurrence was often observed. The preservation of the balance of this unstable body is, however, effected by the long third pair of walking-legs, which project backwards in the direction of the main axis of the body. They seem quite sufficient to counteract the toppling forward of the body referred to, which may therefore not have been so accidental as it seemed. It was observed also that the body could be made to rotate on its long axis by the movement of these legs, as they are directed away from each other posteriorly. Even with these steering organs, however, the activity of the exopodite is not at all proportionate to the progression of the body, and suggests a respiratory instead of, or in addition to, a locomotory function.

These phyllosomas at first sought the light rather quickly, and crowded in a dense mass to a corner of the tank, which at certain times was well lighted. Later, they were found throughout the water at all distances from the surface, and some of them were observed to seek the bottom and come up again. A number, at about the same stage of development, were put in a small glass vessel for better observation, and it was very easily seen, by altering the source of illumination, how readily they sought the light. For about six days they swam about in the tank and then disappeared. Towards the end of that period they seemed to avoid the light. To make certain of this, an active and healthy specimen was carefully watched in a small jar, and it was observed that, in about seven days, it began to avoid the light, and could be made to pass from any one part to another by illuminating the jar from various sides, but, whereas it at first sought the light, it now as obviously avoided it. This behaviour may have been due to abnormal conditions, but, taken in conjunction with the marked absence of later stages among the many thousands caught by the tow-net, would seem to confirm the suggestion that the phyllosomas go to the bottom after this stage. They may do so at each ecdysis.

Phyllosoma of 3·8 mm. [Fig. 21] Pl. 15.

The phyllosoma nearest the first in point of size is a single specimen, procured 50 miles south-east of Table Bay, by a tow-net on the beam of a trawl, working at a depth of 230 fathoms. It is somewhat imperfect, antennules and the distal end of the third maxillipede being broken off; the other features resemble those of the phyllosoma of 1·7 mm.

The endopodite of the *antennæ* is relatively large and has a distinct division halfway between the origin of the exopodite and the base of the flagellum. The exopodite is relatively smaller, being now only about half the length of the endopodite. The parts immediately surrounding the mouth (upper lip, *mandible*, lower lip, and *maxillæ*) are, so far as could be made out, similar to those of the first phyllosoma, but in relation to the cephalic shield, which has now grown very large, occupy a relatively small area of the under surface, the distance between the outer edges of the maxillæ being contained about 5 times in the breadth of the shield, in place of about 3 times, as in the first phyllosoma.

The *second maxillæ* are not different from those of the previous stage. They are slightly larger, being 0·16 as compared with 0·11 mm. in the first stage.

The *first maxillipede* seems to be entirely absent.

The *second maxillipede* resembles that of the previous stage in relative length of segments and in arrangement of setæ.

The *third maxillipede* has the first four segments in the same proportion as before, and there is as yet no trace of an exopodite.

The *first pereiopod* is 5·23 mm. in length—that is, the length of the body (3·8) is contained in it 1·37 times, whereas the length of the body in the preceding stage is contained in the length of its first pereiopod 1·7 times. The length of this appendage is therefore relatively less than in the preceding stages. This relative shortening has taken place least of all in the first and last segments, next in the third and fourth, then in the second, the greatest relative shortening being in the fifth segment.

The *second pereiopod* is very similar to the first, but is somewhat longer by about half a millimetre. The increase is in the fifth segment, which is ·45 mm. longer than in the last appendage.

The *third pereiopod* differs little from the two preceding. There is now a setose exopodite, considerably shorter, however, than those of the preceding pereiopods.

The *fourth pereiopod* consists of a short unsegmented limb 1·28 mm. in length; about ·4 mm. from its base there is a short exopodite ·22 mm. in length.

A great development of the digestive gland has taken place. The posterior lobes have not changed much, and are still quite separate from the main mass. The anterior lobes can also be readily made out, but the lateral lobes are much enlarged and have lost their trilobed condition.

Phyllosoma of 24 mm.

The cephalic shield has increased in relative size, being about 16 mm. broad and the same in length, or 1½ times in the total length of the body. It extends backwards over the thorax to about a line joining the anterior points of the insertion of the first pair of walking-legs.

There is no trace of spines on the dorsal side of the shield. Anteriorly it is produced as a prominence, on which the base of the eye-stalk is inserted.

The *antennules* are three-jointed and have two terminal flagella, the outer extending 1 mm. beyond the peduncle of the antennæ.

The *antennæ* are about twice the diameter of the antennules. There are three well-marked segments, the first of which is shorter than the second, which is equal to the third; the last is terminated by a very strong spine on the inner side. Just beyond it is a joint in the flagellum, the breaking joint in the adult, and the segments of the flagellum begin to show faintly at some distance from it. The first section of the appendage, fused to the body and containing the antennal gland, shows no trace of demarcation from the head region. There is no trace of an exopodite. The upper lip, *mandibles*, and *first maxillæ* form a mass round the mouth, now smaller in proportion to the head region, being about 9 times in the breadth of the shield.

The *second maxilla* (fig. 22, p. 111) has increased greatly, chiefly in its distal segment, which has altered also much in shape. It has become expanded and produced posteriorly, so as to assume a foot-like shape. The first segment is also enlarged and slightly produced anteriorly.

The *first maxillipede* (fig. 23, p. 111) now appears, or rather reappears, in the form of a small stump, with two slight projections. It has, however, altered its position, being removed from the base of the second maxillipede and nearer that of the second maxilla, slightly overlapping it on the inner side. The rudiment of the exopodite is well marked under the cuticle.

The *second maxillipede* consists of five distinct segments as before, but about the first third of its length is a slight bulging on the posterior side, with a smaller one a little further on the anterior ; these are apparently the first traces of the joint and exopodite which appear at this point in later stages.

The *third maxillipede* is very long and consists of seven distinct segments ; there is no trace of an exopodite, except a slight bulging as before.

The abdominal region consists of four segments provided with pleopods with a simple biramose termination, the last with uropods and the terminal telson.

Phyllosoma of 26 mm.

Does not differ much from that of 24 mm.

Phyllosoma of 33 mm.

This stage is well characterised by the appearance of the gills, the rostral elevation, and the demarcation of the first segment of the antenna from the body. A further description of these will be given in considering the next size, of which more perfect specimens are available and which does not seem to differ essentially from this stage.

Phyllosoma of 35 mm. [Fig. 24] Pl. 16.

The total length is 35 mm. The length of the shield is 21 mm., breadth 22 mm., and it reaches to a line joining the centre of the bases of the second pereiopods. The greatest breadth of the thorax is 10·8 mm.

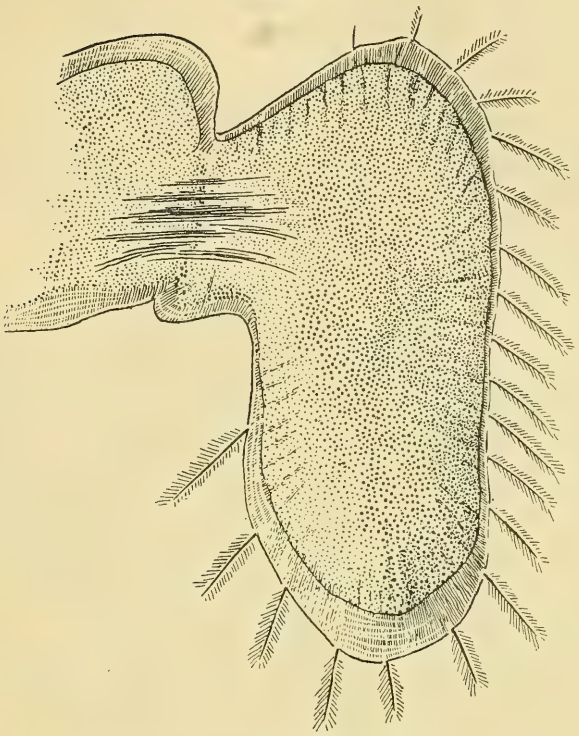
A feature not apparently observed in any phyllosoma hitherto described is the beginning of the rostral elevation, not a simple prominence as in the adult, but having a central projection with one in each side (fig. 25).

The liver is well developed and consists of numerous diverticula.

The eyes are on long stalks with a constriction near their distal end.

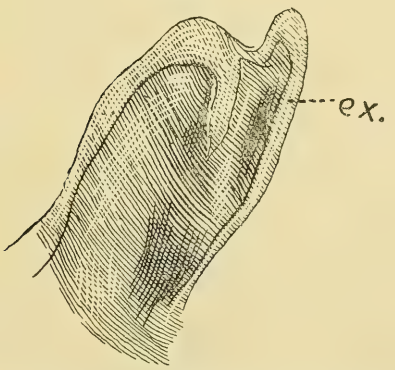
The *antennules* are well developed; the flagella are thick-segmented and

Fig. 22.



Second maxilla of Phyllosoma of 24 mm. × 97.

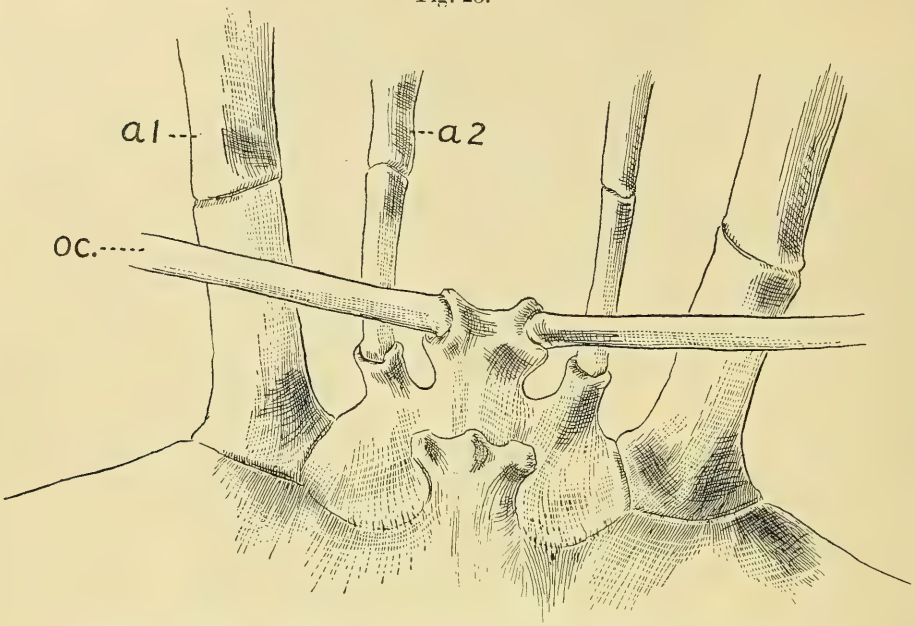
Fig. 23.



First maxillipede of Phyllosoma of 24 mm.

extend beyond the fourth segment of the antenna by about a third the length of the inner.

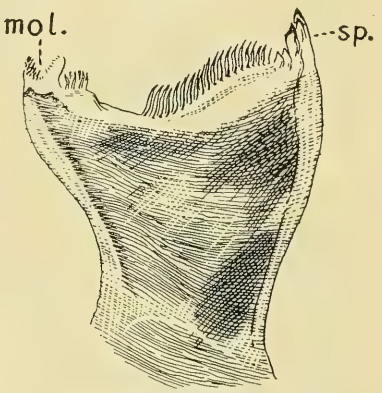
Fig. 25.



Anterior dorsal surface of Phyllosoma of 35 mm., showing rostral elevation.

The *antenna* consists of a basal segment, in which is lodged the antennal gland, and which can be seen to be marked off from the body.

Fig. 26.

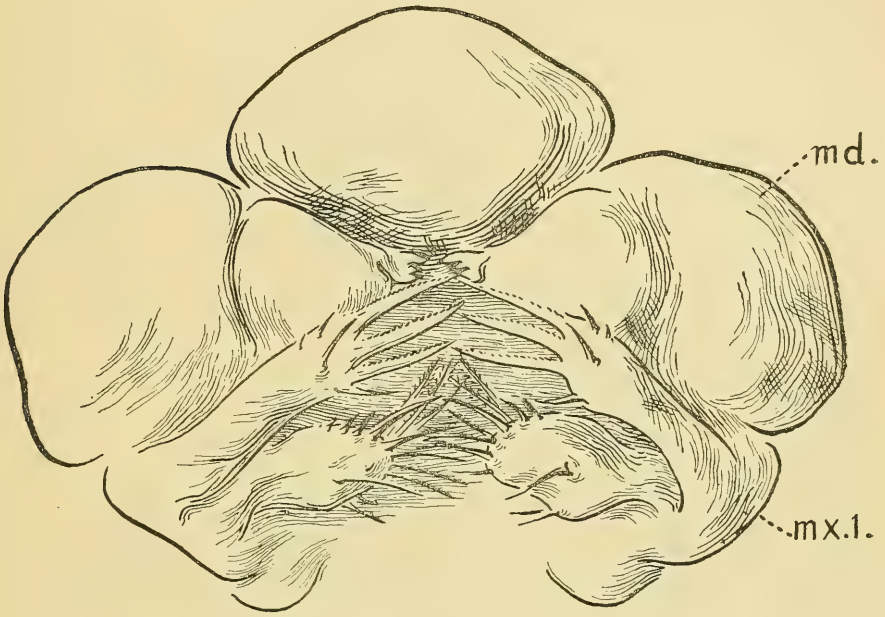


Mandible of Phyllosoma of 35 mm.

The *mandibles* (figs. 26, & 27, *md.*) are well developed, but of the same type as has been seen throughout. Each consists of a short undivided and

unbranched limb, the distal end of which is chisel- or gouge-shaped and lies almost at right angles to the body, so that the outer edge alone is seen when the animal is viewed from below (fig. 27, *md.*). At this outer edge the stout tridentate spine, already noted in an earlier stage, may be seen ; it is followed by two short, rather blunt and thick spines, after which a series of longer, thinner, and sharper spines extending to beyond the middle of the mandible-edge, which may be described as the cutting part. Here they abruptly cease, so that it appeared at first as if they had been broken off, but this was observed

Fig. 27.



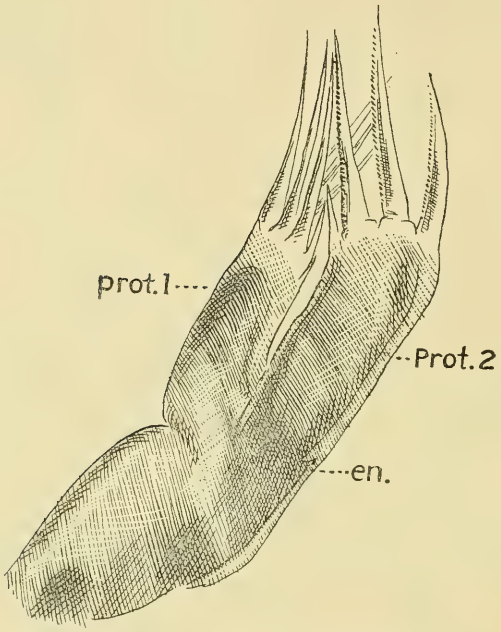
Mouth-parts of Phyllosoma of 35 mm.

also in other specimens and may be natural. The spines towards the middle are somewhat hook-shaped. After the interval devoid of spines there is another but smaller group of spines, close to the base of what may be termed the molar part of the mandible (fig. 26, *mol.*). This last is a characteristic cup or groove-shaped structure with projecting sides, forming a well-marked concavity, in which are situated a number of closely-set short spines, the whole forming a distinct projection which is reflected in the sub-cuticular tissue. This projection is of importance, as, later on, it apparently forms the flat molar surface of the adult mandible or part of it.

The *first maxilla* (figs. 28, & 27, *mx.*1) is of interest chiefly in the appearance for the first time of a trace of the endopodite, not previously recorded in any phyllosoma. It is in the form of a small projection at the base of what is

commonly regarded as the second segment of the protopodite. The spines at the ends of these segments of the protopodite are very well developed; on the first there are about half a dozen, long and rather slender, with

Fig. 28.



First maxilla of Phyllosoma of 35 mm.

lateral projection. A few short spines are inserted near the base. The second is provided with three well-developed spines, with lateral projections and one or two small spines occur at their bases.

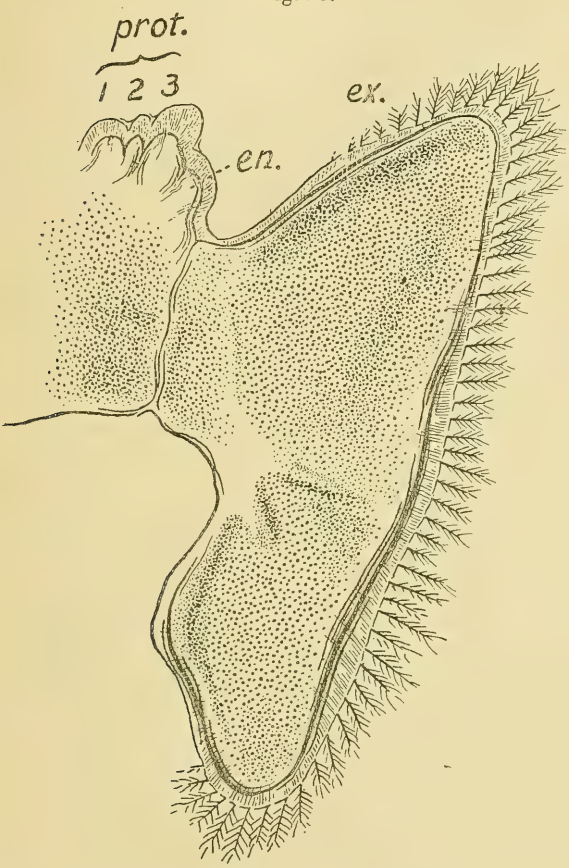
The *second maxilla* (fig. 29) now shows four rudiments situated at its base, representing what are to become the endopodite and the three endites of the protopodite of the adult.

The *first maxillipede* (fig. 30) is furnished with a prominent exopodite and an epipodite. The differentiation of the endopodite and protopodite appears under the cuticle, but there is no division of the latter in two sections.

The *second maxillipede* consists of five segments: the first is not provided with a spine, but has the rudiments of an epipodite; the second has, about its middle, a similar vesicular structure which corresponds to the exopodite of the other appendages. The distal end of the penultimate segment is provided with two strong bent spines, between which the short terminal joint with its strong spine can be bent.

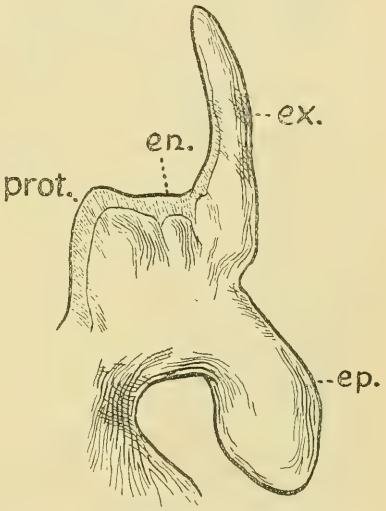
The *third maxillipede* is very long, and consists of five distinct segments: the first has a gill and spine; the second has the rudiment of an exopodite in the middle of its length, but no division; the third is short, the fourth is long and provided with numerous hair-like setæ. The third maxillipede of the puerulus and the adult has seven segments, of which the fourth is the longest, and the proportions are very different from those of this, the oldest

Fig. 29.



Second maxilla of Phyllosoma of 35 mm.

Fig. 30.

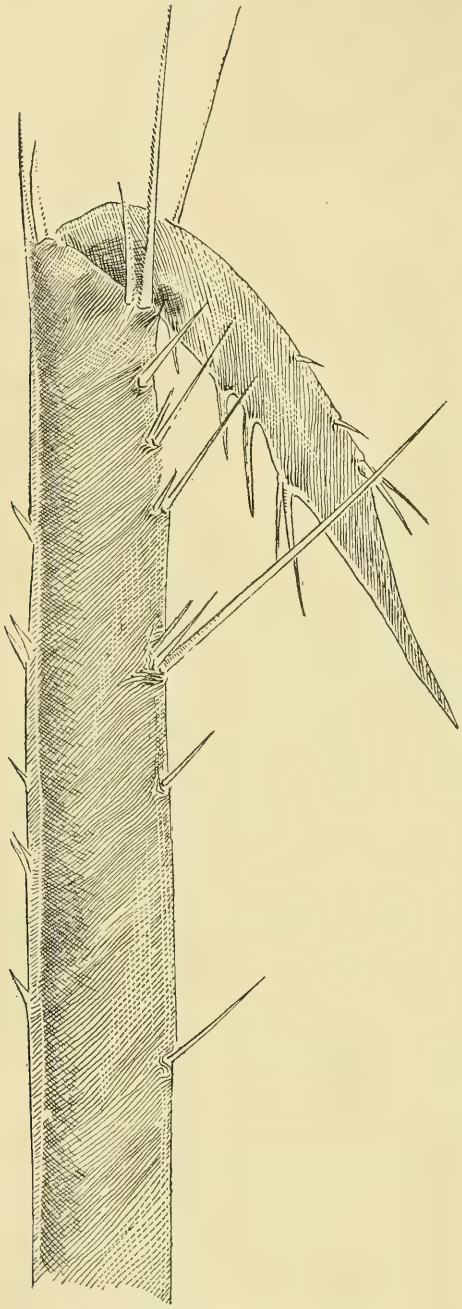


First maxillipede of Phyllosoma of 35 mm.

phyllosoma procured. Transition stages would probably show a great shortening of the second segment, a division near the proximal end of the third segment, and a very great shortening of the penultimate segment, making seven segments in all.

The *pereiopods* have well-developed gills (fig. 43, p. 120)—one podobranch with epipodite, one arthrobranch, and two pleurobranchs. The position of

Fig. 31.



Distal end of second walking-leg of Phyllosoma of 35 mm. × 25.

the pleurobranch and arthrobranch will be described in more detail in connection with those of the puerulus, in relation to which they are of importance. It is of interest to note that this and the succeeding legs are terminated by a claw of a sub-chelate type, the last joint being bent over against the preceding (fig. 31).

There are well-developed exopodites on all of the pereiopods except the fifth, where there is a very small rudiment; this rudiment, like the rudiment in the third maxillipede, resembles the vesicular structure which represents the first appearance of a gill, and suggests that the exopodite may represent a modified gill. The third segment of the fifth pereiopod is relatively long.

The pleopods are present and well developed; their exopodites and endopodites are about equal in size, and in the latter is an appendix interna devoid, however, of setæ and hooks.

The two chief spines on the upper surface of the telson are present, and the margins of telson and uropods are markedly denticulate.

The Rev. T. R. R. Stebbing (6) to whom, some years ago, I submitted a specimen very similar in general appearance and size, compared it with *Phyllosoma longipes*, Milne Edwards (5), and a phyllosoma described by Claus (3), and pointed out certain differences between them. That it is a stage in the life-history of *Jasus lalandii* can only be fully determined by a more complete series of specimens connecting it with the "puerulus"

stage. One characteristic seems to indicate that it is not so, namely, its much greater total length (from anterior end of carapace to posterior end of telson) than that of the puerulus or even later stages of *Jasus lalandii*, and this objection seems to be further strengthened by the recent observations of Bouvier (1) on the larval stages of *Palinurus vulgaris*. He has found what he regards as a complete series of stages between the early phyllosomas and the puerulus stage, there being a gradual increase in size in the total length, that of the oldest phyllosoma being equal to that of the puerulus. The objection, however, disappears when we remember that the total length of the phyllosoma includes the head region between the anterior end and the first maxillipedes. This region, which is nearly half the total length in a phyllosoma of 35 mm., must become enormously reduced before the adult stage, to whatever genus or species it may belong, is reached. The thoracic region also becomes relatively shorter as we advance from the first phyllosoma stage, and the only test of age in terms of length would appear to be in the abdominal region.

Puerulus of 22–26 mm. (Pl. 12 ; [Fig. 32] Pl. 17.)

This stage is transparent, but has still the characteristic red spots of the phyllosoma. These are very marked in the living state, but soon disappear on the death of the animal, if not kept in darkness. They occur chiefly on the under side of the body, as shown in the figure (Pl. 12), which was drawn by Mr. Birbel soon after the animal was captured.

The carapace on its upper surface is almost flat, being slightly convex in the cardiac region. The sides are bent downwards so as to be almost at right angles to the upper surface, but there is no very distinct ridge between sides and upper surface. Posteriorly the sides are not so well developed, and leave the gills partly exposed. There are slight but distinct traces of a cardiac and a pair of branchial grooves.

A few spines only are present. The most outstanding are the frontal or post-rostral. They project over the bases of the eye-stalk, pointing forwards and slightly inwards. Immediately behind them is a smaller pair, projecting forwards over the bases of the first. A little to the outside of this second pair, and behind the middle of each eye-stalk, is a somewhat larger (gastric) spine, behind which, and a little towards the side, is a strong (branchial) spine, from which the lateral ridge commences. Below the eye in the hepatic region is a strong spine. There is a single low median spine over the gastric region, and, posterior to it, towards the cardiac region, a pair of small spines, between which and the ridge spine is another small spine over the branchial region. Thus there are two pairs of frontal spines, three gastric, two cardiac, two pairs of branchial, one hepatic, corresponding to

the largest spines of the adult. No other spines were seen on the carapace. There are no sternal spines.

The rostrum is a very small simple projection, and does not appear to meet the ocular segment.

The *antennules* (Pl. **13.** fig. 33, *a.* 1) are relatively short, the peduncle reaching to about the first third of the fourth segment of the antennæ. The flagella are, however, relatively stouter and longer than in the adult.

The *antennæ* (fig. 33, *a.* 2) are much longer than in the largest phyllosoma. The peduncle has the chief large spines of the adult, but the smaller scale-like spines are not yet developed.

The *mandibles* (Pl. **13.** fig. 34), of all the other parts, show the greatest and most abrupt change from the phyllosoma conditions, but have not as yet assumed the adult characteristics. They thus present an instructive intermediate stage. The change is doubtless associated with the assumption of a ground habit, the mouth-parts being used for crushing up the harder shells, etc., on which the animal now feeds. The setæ, so prominent in the phyllosoma, are replaced by a thick cuticle. The incisor part can still be distinguished from the molar; it consists of a broad cuticle with two slight projections, which in some are hardly distinguishable, but are clearly represented in the subcuticular tissue, and, in later stages, become the two prominent teeth of the cutting-edge of the adult mandible. The molar part is in the form of a blunt well-marked projection, which has now come to lie somewhat behind the cutting-edge. In other words, the free edge of the mandible of the phyllosomas, consisting of cutting and mandibular parts, instead of forming a slightly curved edge, is now bent so as to form almost a circle. This can be clearly seen when the mandible is viewed from its distal extremity. It would appear therefore that the molar part of the mandible of the phyllosoma in the course of its development turns backward behind the cutting-edge, and assumes the flat hard character of the molar part of the adult mandible. The endopodite of the mandible, no trace of which was found in the phyllosomas, now appears, but consists only of one distinct segment. The beginning of the mandibular spine is also seen.

The *first maxilla* (Pl. **13.** fig. 35) has now assumed the foliaceous form of the adult. The protopodite is deeply cleft into two segments, and near the base of the second a small endopodite appears, about half of its base arising from the inner side, so that it is not clearly seen when viewed from below. All the spines have disappeared, though a few were seen on the anterior border of the coxopodite and basipodite on one specimen. The appendage is now removed from the base of the lower lip by a distance equal to the length of the coxopodite.

The *second maxilla* (Pl. **13.** fig. 36) has the three endites of the protopodite relatively larger than in the adult condition and provided with a few setæ. The endopodite is relatively much smaller and is triangular instead of convex,

as in the adult; it has only a few setæ. The exopodite (scaphognathite) is well developed and provided with feathered setæ.

The *first maxillipede* (Pl. **13.** fig. 37) does not differ essentially from that of the adult, but the endopodite is smaller and lies more to the inner side of the exopodite.

The *second maxillipede* (Pl. **13.** fig. 38) differs from the adult condition in that the flagellum of the exopodite is not segmented, and the last segment of the endopodite is provided with a short spine at its tip.

The *third maxillipede* (Pl. **13.** fig. 39) is characterised by a very short exopodite, consisting of one undivided segment, about half the length of the first segment of the endopodite, which lies alongside of it. The last three segments of the endopodite are provided with long serrated spines on their inner surface.

The *first pereiopod* (Pl. **13.** fig. 40) shows the long basipodite of the phyllosoma reduced to a mere ring of chitinous tissue, narrower on the upper side than on the lower. At its narrowest point there is a projection of irregular outline, and of a clear refractile substance; this appears to be the remains of the exopodite.

Some of the spines of the limbs are of interest. In the phyllosoma there occurs, at the distal end of the fourth segment of the leg, two spines evidently of a defensive function. Here, as in the adult, their position is taken by the projection, on which is the socket of the "ball-and-socket" joint, between the segments, and their place is taken functionally by a single median spine which now appears for the first time. It would appear that this pair of defensive spines of the phyllosoma may be transformed to form the joint of the adult, and this may be true also of all the other joints of a similar nature.

Fig. 42.

Epimera of oldest Phyllosoma, Puerulus, and adult.

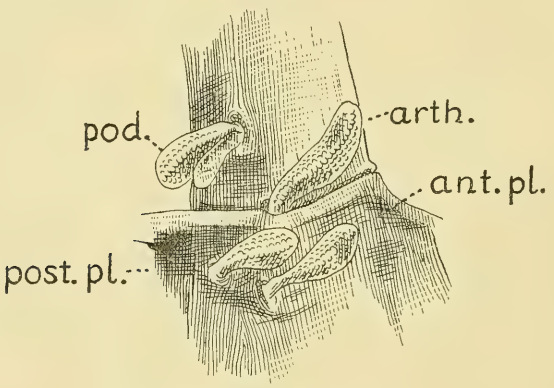
The *pleopods* (Pl. **13.** fig. 41) are all more or less similar, and have large flat exopodites and endopodites, provided with feathered setæ. There is a coupling projection on the inner side of each endopodite, provided with a feathered spine and hooks at its base.

The telson has a second pair of spines, rather faintly marked, situated behind the pair already seen in the last phyllosoma.

The shape of the epimeron is intermediate between that of the last phyllosoma and the adult (fig. 42).

The gills of the puerulus are of interest, as they seem to point to the solution of a difficulty connected with the difference in position of the gills in the phyllosoma and the adult. In the adults of the Scyllaridæ and all decapods generally there are (it is believed) one pleurobranch, two arthrobranchs, and one podobranch, while in the larval forms (phyllosomas) there are clearly two pleurobranchs, one arthrobranch, and one podobranch. This difference between the young and adult forms is well known, and it is desirable to ascertain whether the adult condition is a primary or secondary one. There can be no doubt that the arthrobranch of the phyllosoma is placed on the joint (fig. 43) and that it is well separated from the two pleurobranchs. These latter occur on the dorsal side of the flattened thorax, and the name is therefore not strictly accurate. The real side or pleuron of

Fig. 43.



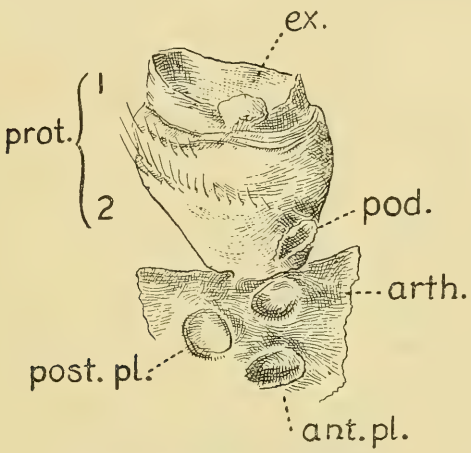
Gills of Phyllosoma of 35 mm.

the thorax is still in the form of a thick cuticular rim, which, although rather thinner at the insertion of the appendage, still forms a marked ridge separating the arthrobranch clearly from the pleurobranchs, so that frequently, when viewed from above, only part of the arthrobranch can be seen, protruding from under the edge of the thorax, which overhangs the base of the limb. The two pleurobranchs (on the 2nd to the 4th walking-legs) are at some distance from this edge and are thus clearly separated from the joint and its gill-rudiment. They are also well separated from each other, and it is particularly to be noted that the posterior is distinctly nearer the side of the body than the anterior. This has been noted in all the phyllosomas examined and may occur in other phyllosomas, though the point has not been particularly noted.

In the puerulus stage the thoracic region has become much deeper,

narrower, and shorter, and this has brought about a considerable change in the relative positions of the gills. The rim of the thorax has disappeared as such, and no longer forms a projection separating the pleurobranchs from the arthrobranch. The position of the two pleurobranchs with reference to each other has changed. The first or anterior, formerly only slightly further from the arthrobranch than the second, is high up on the now vertical wall of the thorax, while the second has remained low down. This rearrangement of the pleurobranchs is, of course, in co-ordination with the shortening and heightening of the side of the thorax (fig. 44).

Fig. 44.



Positions of gills of Puerulus.

With the disappearance of the rim of the thorax there is no clear separation between the single arthrobranch and the nearest pleurobranch (the posterior), so that it is now scarcely possible to draw any clear distinction between arthrobranchs and pleurobranchs, and the functional joint has now become enlarged to include the bases of these two gills. When calcification of the sides of the thorax sets in, in later stages, the anterior gill is completely separated from the other two. The adult condition may therefore be described as brought about by the posterior pleurobranch of the phyllosoma becoming an arthrobranch in the adult. It may, however, be noted here that it is not quite correct to state that there are two arthrobranchs in *Jasus*, as the posterior of these is marked off from the joint by a slight calcification clearly seen in cast shells.

In the next stage of *Jasus lalandii* the branchiæ have not altered much in their position and relation to the coxa and its proximal joint. The cuticle generally has become calcified, but the pleura only slightly. A slight deposit of carbonate of lime is seen below the base of the first or anterior pleuro-

branch, separating it still more effectively from the second. Ultimately the calcification extends completely round the first and over the pleura generally, and the anterior pleurobranch is still higher up the side.

The puerulus here described does not quite agree with that described by Bouvier (2) from the island of St. Paul, and suggested by him to be that of *Jasus lalandii*. Thus, there is no very distinct dorso-lateral ridge, and there are fewer spines on the dorsal region of the carapace ; the exopodite of the third maxillipede does not nearly reach the articulation of the ischiopodite with the meropodite as in his specimens. The frontal spines are, however, slightly convergent, and it may represent an earlier stage than that described by Bouvier. Gruvel (4) also describes some young forms of this species from the island of St. Paul, but not in sufficient detail for a comparison with our specimens.

Review of Results.

The larvæ of the first and second stages of *Jasus lalandii* can readily be hatched out from the egg. Larvæ of the second stage were found in abundance in the inshore waters during the summer months, and a much smaller number of more advanced stages (up to 37 mm. in length) in deep waters. The puerulus stage can be found close inshore. These were all found on the west coast of S. Africa, and are regarded as stages of *Jasus lalandii*, the only known representative of the Scyllaridea in this region, where it occurs abundantly.

Three other kinds of phyllosoma and two kinds of puerulus occur on the south and east coasts, apparently belonging to other South-African Scyllaridea (*Palinurus*, *Panulirus*, and *Scyllarides*).

The appendages of the first or naupliosoma-stage are described and figured. The second or phyllosoma-stage (1·7 mm.) differs from it in the absence of the swimming setæ of the antennæ, the appearance of the flagellum of the endopodite, the presence of olfactory (?) filaments on the antennules, etc. A phyllosoma of 3·8 mm. shows relative increase in size of shield, decrease in length of walking-legs, diminution of the exopodite of the antenna, absence of first maxillipede, appearance of the fourth walking-legs, etc. A phyllosoma of 24 mm. shows still greater relative increase in size of shield, flagella appear on antennules, antennæ are three-jointed and their exopodites have disappeared, the distal part of the maxilla has broadened out and expanded posteriorly to form the scaphognathite, the first maxillipede reappears as a simple stump with two slight projections, and pleopods appear as simple biramose organs. A phyllosoma of 26 mm. shows no essential change, but in one of 33 mm. the gill-rudiments appear and a rostral elevation with three prominences, the middle one of which may represent the rostrum, the other two the ocular spines. The mandible consists of three strong spines, followed by a series of small spines, inserted on an elongate edge and

separated by an interval from a molar-like part. A trace of an endopodite appears on the second maxilla, and the endopodite and endites of the protopodite appear on the second maxilla. The first maxillipede has the beginnings of an exopodite and an epipodite.

The puerulus shows the typical characteristics of this stage—transparent soft cuticle, few spines on carapace, bases of the third maxillipedes well separated, antennular peduncle short, coupling-hooks on the appendix interna. The puerulus in its natural state, though transparent, is not colourless and has the red spots characteristic of the phyllosoma. The condition of the mandible indicates the method of transition between the phyllosoma and adult state, the molar part becoming turned round, somewhat behind the incisor part.

Observation of the habits of the living animal shows that the naupliosoma stage moves towards the light and undergoes ecdysis without descending from the surface of the sea. The second stage at first also seeks the light, but later on avoids it, and seems to descend from the upper layers of the water on ecdysis.

The exopodite on its first appearance has the same general appearance and position with regard to the limbs as the rudiments of the gills. It is therefore suggested that the exopodite has arisen from a former gill. Observation of the living naupliosoma seems to indicate that the exopodite has still an important respiratory function.

A feature common to all the stages of the phyllosoma examined is that the last pair of well-developed walking-legs are relatively long and, probably in all stages, act as steering-organs, as was observed to be the case in some living specimens. The lengthening of this limb is chiefly in the first segment of the endopodite, and this may prove to be a diagnostic characteristic of the species.

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EXPLANATION OF PLATES AND TEXT-FIGURES.

Plate 12.

Puerulus of *Jasus lalandii*, showing natural colours, ventral aspect.

Plate 13.

Fig. 1. Antennule of the Naupliosoma.
2. Antenna „ „
3. Mandible „ „
4. First maxilla „ „
5. Second „ „ „
6. First maxillipede of the Naupliosoma.
7. Second „ „ „
8. Third „ „ „
9. First pereiopod „ „
10. Second „ „ „
11. Third „ „ „

Plate 14.

Fig. 12. Phyllosoma of 1·7 mm.

Plate 13.

Fig. 13. Antennule of Phyllosoma of 1·7 mm.
14. Antenna „ „
15. Mandibles, first maxillæ, second maxillæ, and first maxillipedes of Phyllosoma of 1·7 mm.
16. Second maxillipede of Phyllosoma of 1·7 mm.
17. Third „ „ „
18. First pereiopod „ „
19. Second „ „ „
20. Third „ „ „

Plate 15.

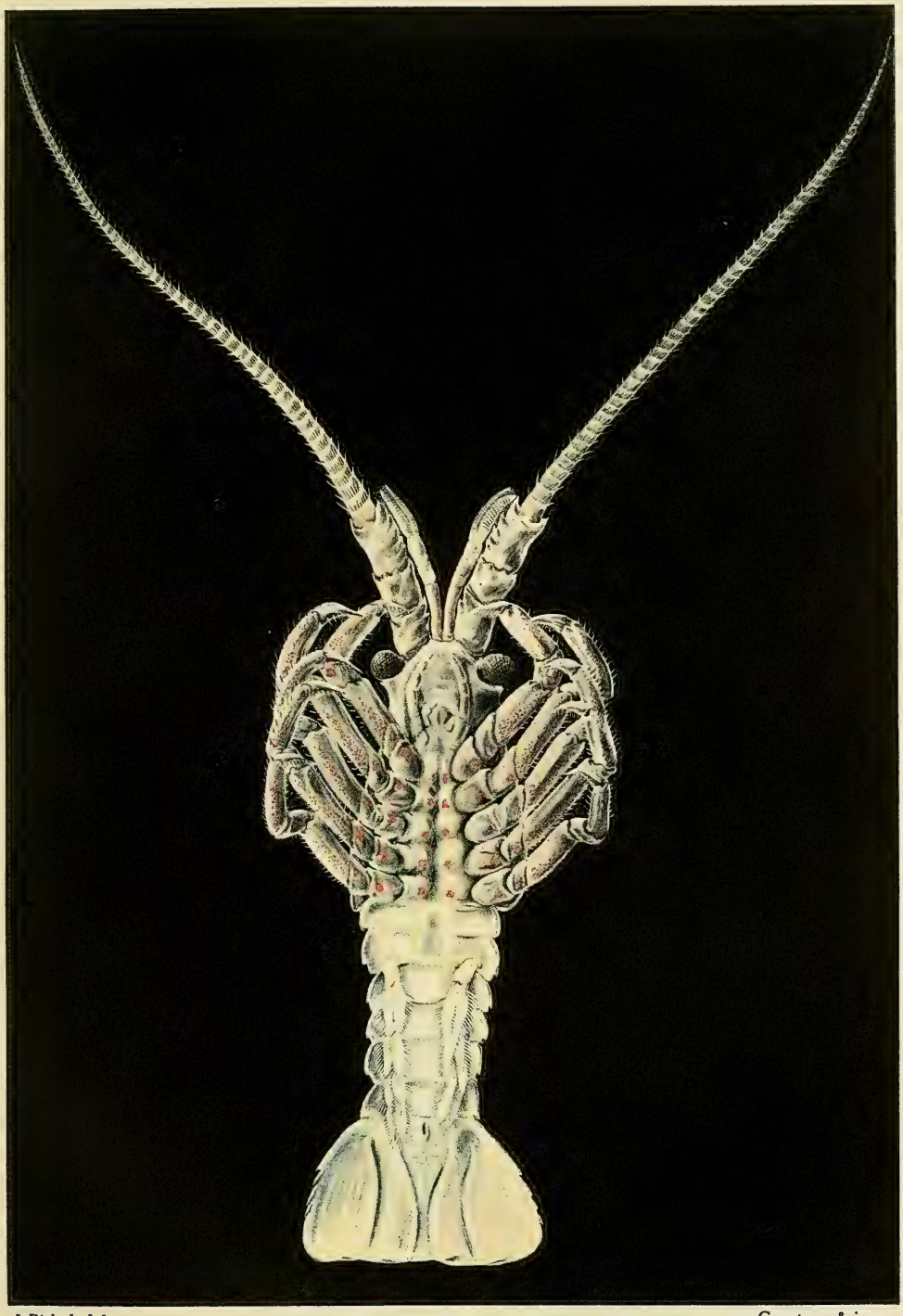
Fig. 21. Phyllosoma of 3·8 mm.

Fig. 22. Second maxilla of Phyllosoma of 24 mm. Page 111
23. First maxillipede „ „ „ 111.

Plate 16.

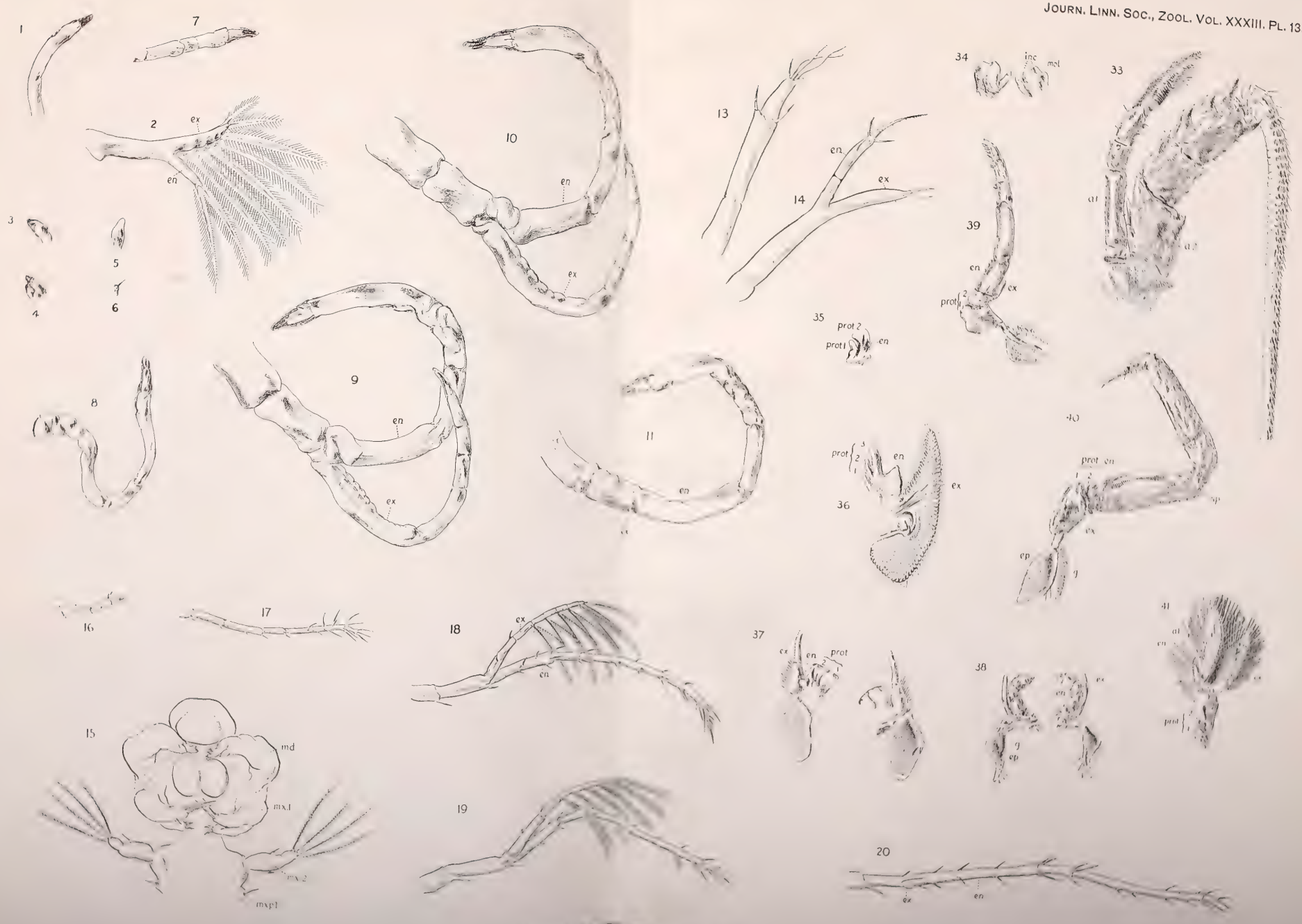
Fig. 24. Phyllosoma of 35 mm.

Fig. 25. Anterior dorsal surface of Phyllosoma of 35 mm., showing rostra elevation. Page 112.
26. Mandible of Phyllosoma of 35 mm. „ 112.
27. Mouth-parts „ „ „ 113.
28. First maxilla „ „ „ 114.
29. Second „ „ „ „ 115.
30. First maxillipede „ „ „ 115.
31. Distal end of pereiopod of Phyllosoma of 35 mm. „ 116.

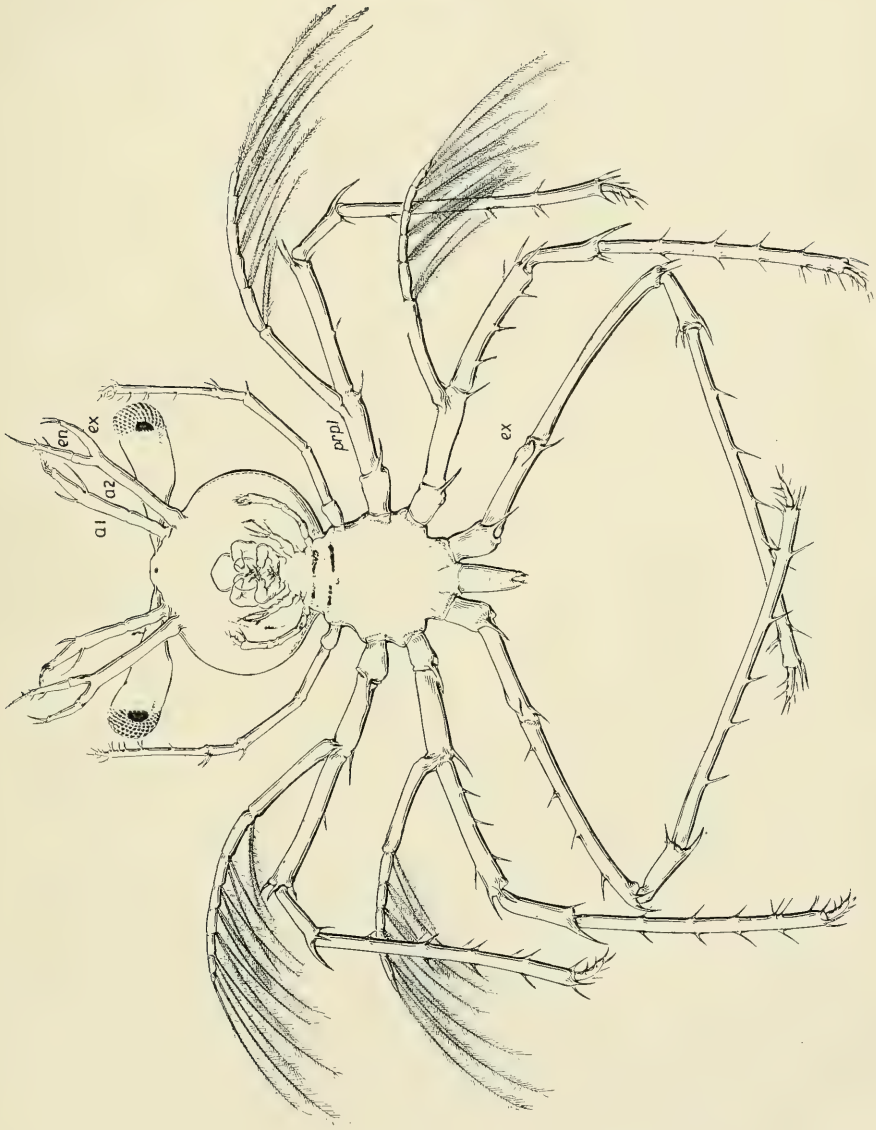


J. Birbel, del. Grout, sc. & imp.

JASUS LALANDII.



JASUS LALANDII (Milne Edw.) Ortm.



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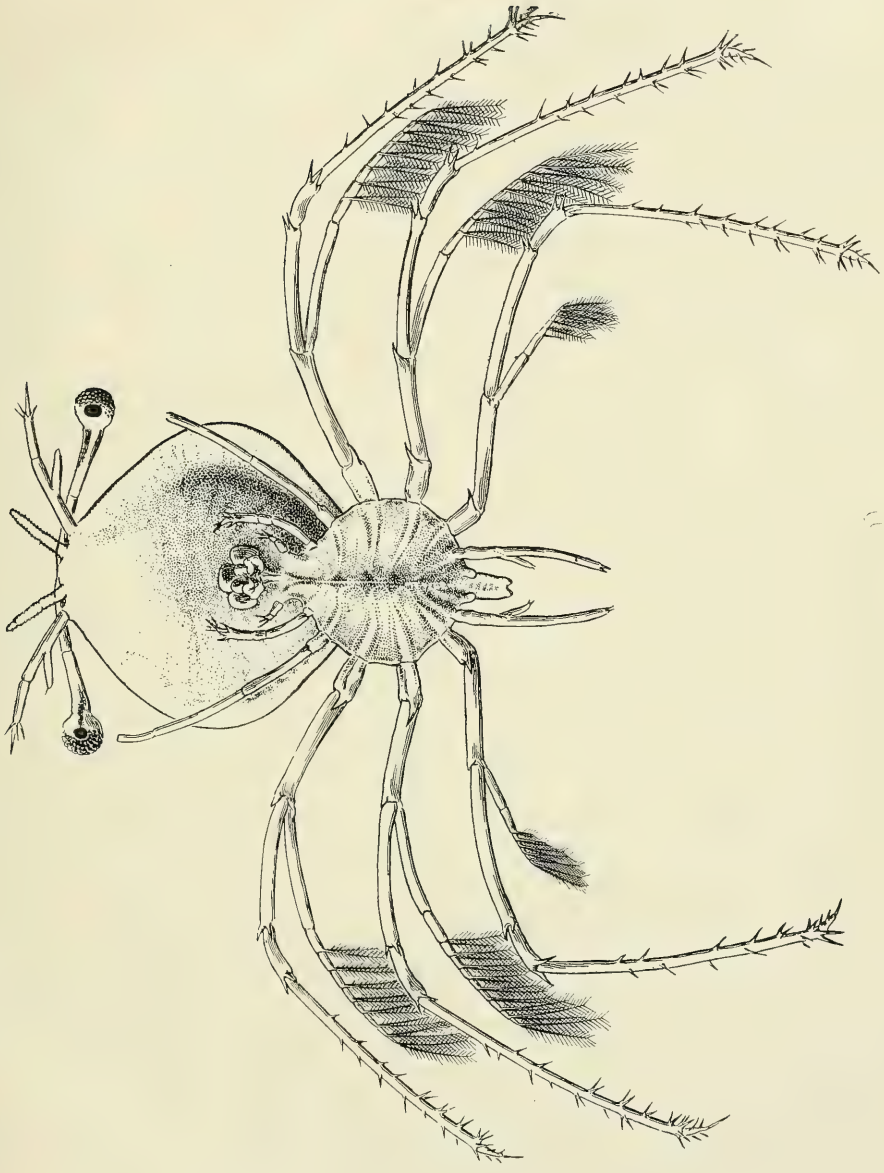

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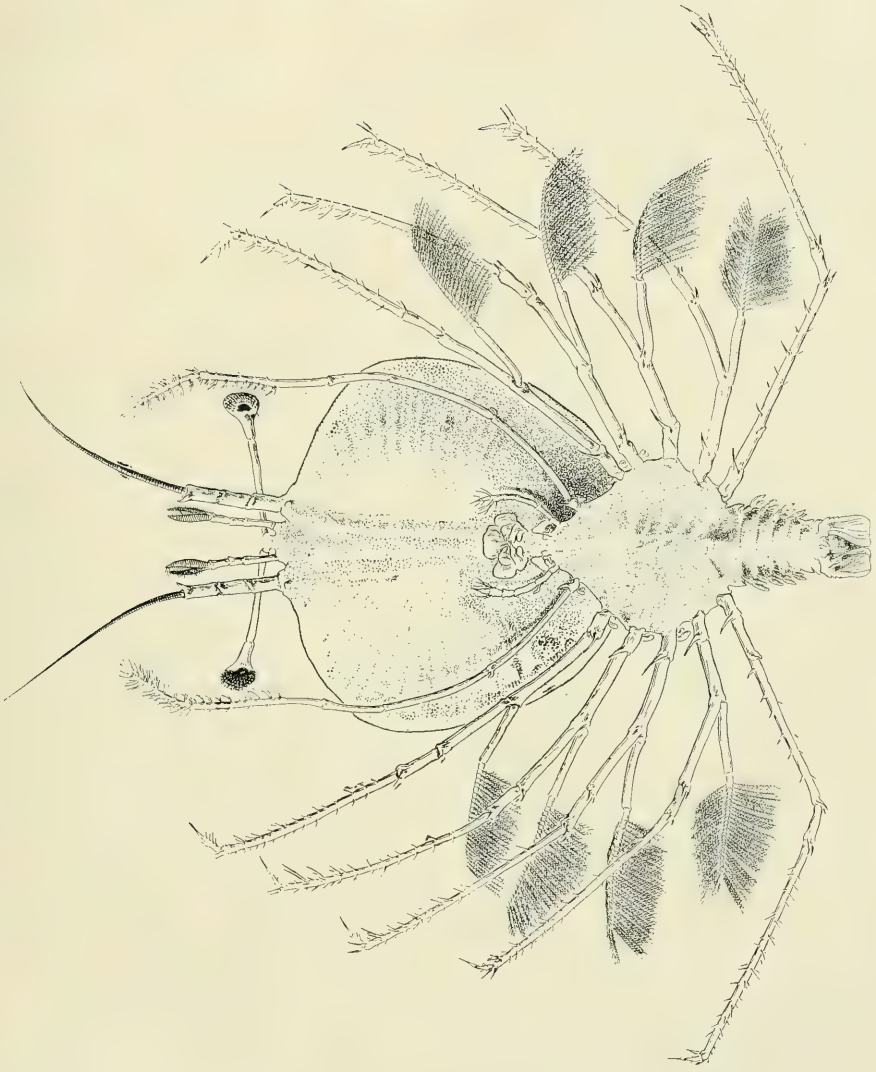

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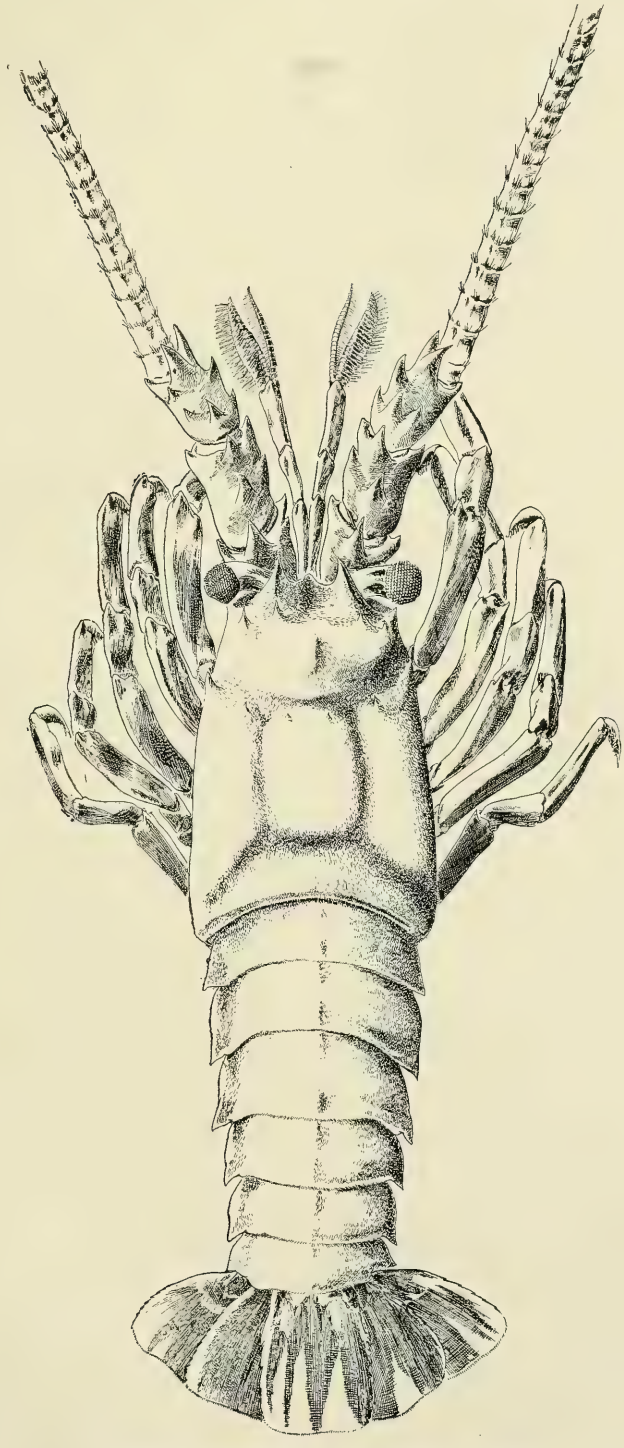

JASUS LALANDII (Milne Edw.) Ortm.

PLATE 17.

Fig. 32. Puerulus of 22 mm., dorsal view.

PLATE 13.

Fig. 33. Antennule (*a.* 1) and Antenna (*a.* 2) of Puerulus of 22 mm.
34. Mandible of Puerulus of 22 mm.
35. First maxilla „ „
36. Second „ „ „
37. First maxillipede „ „
38. Second „ „ „
39. Third „ „ „
40. First pereiopod „ „
41. Pleopod „ „

List of Abbreviations.

a. 1. Antennule.
a. 2. Antenna.
a.i. Appendix interna.
arth. Arthrobranch.
en. Endopodite.
ep. Epipodite.
ex. Exopodite.
g. Gill.
inc. Incisor part of mandible.
md. Mandible.
mol. Molar part of mandible.
mx. 1 & *mx.* 2. First and second maxillæ.
mxp. 1 to *mxp.* 3. First to third maxillipedes.
pl. Pleurobranch.
pod. Podobranch.
prot. Protopodite.
prp. Pereiopod.
sp. Spine.